The quantitative principles of animal growth

J. A. N. Filipe, I. Leinonen, and I. Kyriazakis

School of Agriculture, Food and Rural Development, Newcastle University,
Newcastle upon Tyne NE1 7RU, UK
Corresponding author: Joao.Filipe@newcastle.ac.uk

Abstract

The principles and a quantitative theory of growth for monogastric livestock animals are described here, focusing on the period from birth to slaughter. The theory helps to understand key relationships between the outcomes that may be desired in a production system and their influencing factors, e.g. nutritional, genetic, and environmental, and forms the basis of current mechanistic models for predicting animal performance. We describe general physical, chemical and biological principles that should underlie any description of animal growth; and address growth as a three-faceted problem: 1) growth under 'normal' conditions; 2) growth under 'limiting' conditions; and 3) recovery growth when 'normal' conditions are restored. We propose a theoretical framework that incorporates these situations as facets of a whole, that encompasses growth conditions across modern livestock production systems, and in which terms such as 'normal' and 'limiting' acquire a meaning. To make this framework quantitative, we apply a body of theoretical and empirical principles in the derivation of mathematical models of growth. The usefulness of existing theories and mathematical models depends on the availability of data for testing hypotheses and parameterising models under a range of conditions. A challenge ahead, therefore, is in obtaining extensive data for further testing and consolidating modelling prediction of growth under a wide range of conditions, or as animals respond to change in limitations. Another challenge lies in addressing practical problems posed by heterogeneity in performance within groups of animals: i.e., how to manage groups towards optimal resource use and performance, and how to identify best phenotypical characteristics within breeds, strains, etc. and predict their performance. Further progress will require much greater availability of rich individual data cross-sectioning herds and breeds.

Key words: Pigs; chickens; growth modelling; population modelling; growth restriction; compensatory growth

1. Growth as a journey

Growth is a journey: from conception towards a final size. How the animal travels through this journey depends on what kind of an animal it is and the conditions it is kept in. Not all animals of the same species travel similarly; some animals are genetically determined to grow faster than others, during any or some parts of this journey. The environmental conditions, for example the food offered to the animal and the presence of health challenges, may constrain animal growth and delay the journey (Sandberg *et al.*, 2006). On the other hand, the way an animal reaches a certain point of the journey (i.e., its size and body composition) may define

Chapter 13 In: Paul J. Moughan and Wouter H. Hendriks, ed. Feed Evaluation Science. Wageningen: Wageningen Academic Publishers, 2018

how the animal continues the journey (i.e., its subsequent growth, (Kyriazakis and Emmans, 1992c).

In this chapter, we describe the principles and a quantitative theory of growth in monogastric livestock animals, such as pigs and chickens, focusing on the period of time from birth to slaughter. The theory helps to understand key relationships between the outcomes that may be desired in a production system and their influencing factors (e.g., nutritional, genetic, and environmental) and forms the basis of current mechanistic models for predicting animal performance. We describe general physical, chemical and biological principles that should underlie any description of animal growth; and address growth as a three-faceted problem: (1) growth under 'normal' conditions; (2) growth under 'limiting' conditions; and (3) recovery growth when 'normal' conditions are restored. We propose a theoretical framework that incorporates these situations as facets of a whole, in which terms such as 'normal' and 'limiting' acquire a meaning. To make this framework quantitative, we apply a body of theoretical and empirical principles in the derivation of mathematical models of growth.

Recognising there is variation among animals growing under similar conditions, we discuss population-level descriptions of growth based on phenotypical characteristics, including recent results that predict animal performance as data-based probability distributions both at animal and population levels, providing a phenotypical description of a 'breed'. The models described should apply to most situations in (1) above and some situations in (2) above.

2. Fundamental principles underlying growth

The animal, just like any biological or other system within the known universe, must follow certain fundamental principles of physics and chemistry. Being aware of these principles provide a useful reality check when predicting quantitatively animal performance, and in many cases they provide a natural starting point when building mathematical models for complex biological systems. In spite of this, these are aspects that are surprisingly often overlooked by livestock researchers. In this section, we demonstrate the application of two universally valid principles, namely the law of mass (M) conservation and the law of energy conservation. We also discuss somewhat less precisely determined principles of biological constraints of growth.

2.1 Mass conservation

The universally accepted principle of mass conservation states that for any system closed to all transfers of matter and energy, the mass of the system must remain constant over time, as system mass cannot change quantity if it is not added or removed. The animal cannot be considered as a closed system since obviously there are inputs and outputs of matter and energy to and from the animal. However, following the mass conservation principle, it can be noted that the inputs and outputs, and the change of the mass within the system must be balanced, that is the input minus the output must equal the change in the mass content (either positive or negative).

By definition, the animal is growing (i.e., its mass is increasing) when its material inputs (from feed, drinking water and atmospheric oxygen needed) temporarily exceed the material output (or turnover, in terms of e.g. faeces, urine and respiratory CO_2 and water) (Figure 1). As a

Chapter 13 In: Paul J. Moughan and Wouter H. Hendriks, ed. Feed Evaluation Science. Wageningen: Wageningen Academic Publishers, 2018

result, a necessary outcome is that when the material inputs are limited under constrained conditions (either due to limited supply or limited feeding ability of the animal) the growth of the animal is reduced, unless the outputs are reduced at the same time. Further, after a period of fast growth, the growth gradually decreases as the animal gets bigger. The physical reason for this is that the material output (turnover) increases more rapidly than the material input as the animal's size increases. Finally, as the two flows equalise the animal stops growing, and, as a result, the input and output stop increasing (see section 3).

Modelling (or quantifying) total material flow in to and out of the animal is usually not a practical solution for addressing most scientific questions. Instead, modelling can be focused on single elements which have more meaning in understanding the function of the animal. The main elements forming the animal body are oxygen (O), carbon (C), hydrogen (H), nitrogen (N), calcium (Ca) and phosphorus (P). Together, these elements form around 99% of the body mass (M), and all of them have an essential role in the structure and functioning of the animal, as discussed in more detail below. The principle of mass conservation that was discussed above in the context of the whole body mass is also valid for each of these elements. Therefore, the change (increase or decrease) of the mass of each of these elements in the animal body must be equal to the input minus the output of the element.

The understanding of growth at the level of single elements is useful in itself, but it is biologically more meaningful to focus on more complex compounds formed by these elements, which create the 'building materials' of the animal body. Traditionally in animal science, the growth of the body has been described as a growth of separate components (predominant chemical compounds), namely protein, lipid and water (Kyriazakis and Whittemore, 2005). The remaining body mass consists of different minerals (although part of the minerals is also contained in proteins) and are usually collectively called 'ash' (this is probably due to the fact that in early research work ash could have been easily separated from the rest of the body by combustion, while identifying separate minerals has been more difficult). Although similar components can be identified from inputs (i.e., feed containing protein, lipid and minerals; drinking water), modelling the transformation of these components to the animal body is not straightforward, and, unlike in the case of single elements, it cannot be described solely by the principle of mass conservation. The reason for this is that these compounds go through a complex series of chemical processes before contributing to the animal body as "growth".

As a starting point, the animal diet (material input) contains various plant-based (or sometimes also animal-based) products where the main compounds utilizable by the animals are starch, fats, proteins, sugars and various minerals (which are provided either as part of plant or animal based feed ingredients or as separate additives). In the animal digestion, these are broken down to simpler compounds: carbohydrates (starch and sugar) to simple sugars such as glucose; proteins to amino acids and peptides; and fats to fatty acids and other compounds such as glycerides. Following this, these simple compounds are used in the animal's metabolism to build the main components of the body, while some of the mass of feed is lost for example as a result of incomplete digestion (faeces) or CO_2 as a product of respiration.

The principle of mass conservation can be stated as: let m_i^+ and m_i^- be the rates of mass gain and loss (kg/d) of a certain component i; then the corresponding net rate of mass gain is

$$\frac{dM_i}{dt} = m_i^+ - m_i^- \quad (1)$$

Chapter 13 In: Paul J. Moughan and Wouter H. Hendriks, ed. Feed Evaluation Science. Wageningen: Wageningen Academic Publishers, 2018

which, when positive, implies that the animal has a gain in this component (e.g. increase in calcium through bone growth). If *i* is a chemical element such as Ca, O, or C, it is not lost or gained in chemical reactions, therefore m_i^+ and m_i^- coincide with the input and output; however, if *i* is a compound such as protein or lipid that can be used up or produced in chemical reactions within the animal, then m_i^+ and m_i^- have contributions from these reactions. The rate of gain in *M* of a growing animal is, therefore, a sum of rates of mass gain across a suitably chosen set of animal constituent components (Ω), such as protein, lipid, ash, and water:

$$\frac{dM}{dt} = \sum_{i \in \Omega} \frac{dM_i}{dt} \quad (2)$$

Growth occurs when dM/dt> 0. In practice, we may be able to measure net gains $\frac{dM_i}{dt}$ but not separate flows m_i^+ and m_i^-, which may often result from non-measurable flows and reactions.

2.2 Energy conservation

As discussed above, the growth of the main dry matter components of the animal body, namely protein and lipid, can be seen as a transformation of chemically simpler compounds to a much more complicated form. As a result of this transformation, the content of chemical energy of these complex compounds is also higher than that of their simpler 'building blocks'. Being an open system in terms of the energy flow, the main part of the process of construction of these compounds takes place even before they enter the animal, as it is actually green plants that are responsible for the primary production of these substances by utilizing the solar radiation energy. Animals only 'recycle' these high-energy compounds which they get from plant-based (or already recycled animal-based) feed ingredients. Therefore, the growth of the main dry matter components in the animal body, namely protein and lipid, can be considered as transforming the chemical energy of feed to the chemical energy stored in the body, with the exclusion of necessary losses, such as metabolic heat production. This process necessarily follows another fundamental principle, namely the law of energy conservation, which states that 'Energy can neither be created nor destroyed'. It is extremely important to follow this principle in any mathematical modelling or other quantitative approach describing animal growth; violating it will result automatically in an erroneous outcome.

Many mathematical models describing the growth of animals are based on the overall idea of the intake and partitioning of energy. As seen above, all of the energy needed for growth enters the animal in the form of high-energy compounds in feed. This chemical energy can be quantified as 'combustion energy of feed' (sometimes also called 'gross energy') and is equal to the heat that would be released if the feed eaten by the animal would be combusted. However, not all of this energy is utilizable by the animal. A significant part of it is lost in faeces (as undigested feed), or may be lost (especially in ruminants) as the combustible energy of methane released in the digestion process; a small amount of it can be lost as some high-energy compounds in urine. After these losses, the remaining energy will be available for the metabolic processes of the animal, and is, therefore, called 'metabolisable energy'. This component of the animal energy intake can be considered as a starting point of the mechanistic models for animal growth and performance, and the process describing how this energy is partitioned also specifies the growth of the main dry matter components of the animal body, namely protein and lipid.

The fraction of the combustible energy of feed that is actually metabolized depends on various factors, including the digestion process of the animal. The efficiency of this process depends obviously on the composition of the feed, but there are also differences between animals in how efficiently they can digest different feedstuffs. Feed producers usually provide a uniform value 'metabolisable energy content' of the feed, supposing that this single value would be valid for all animals in any conditions. This is possibly a sufficient approximation for practical purposes, such as a farmer's decision making, but certainly it is an oversimplification for the purpose of scientific research, especially when the differences between individual animals are considered.

To make predictions on animal growth and other functions involving energy flow, the total metabolisable energy entering the animal body (quantified either through measurements, modelling, or simply by relying on the generic figure provided by the feed producer), must be partitioned to various pools or processes. As a general rule, this energy can be partitioned to what is stored in the body (permanently or temporarily) as chemical energy, and to the energy that is lost as heat as a result of metabolic processes. Again, following the principles of energy conservation, these two components must equal the total 'metabolisable' energy the animal has obtained from feed. The energy retained in the body can be divided further to various components or compounds. A common division is to separate the chemical energy retained in proteins and lipid, which are by far the most abundant high-energy compounds in the animal body.

The main problem in modelling the energy flow through the animal is the question of how to further partition the energy that is released as heat. Although all the transformation of chemical energy to heat is a result of metabolic processes occurring in a living animal, it is sometimes considered to be useful to identify the source of that heat more specifically, to produce detailed models of the animal metabolism and growth (Emmans, 1994). Unfortunately, such a detailed analysis is not straightforward, and it is necessarily based on somewhat arbitrary concepts and definitions. For example in many modelling approaches, the metabolic functions are divided into 'maintenance' which is considered to include only that fraction of the metabolism that is necessary to keep the animal alive, while all other metabolic heat production (related to for example growth and digestion) is referred to as 'heat increment' or 'inefficiencies' (Emmans, 1994; van Milgen *et al.*, 2008). Biologically, it is not possible to separate these processes from each other (after all, this division is only made arbitrarily for modelling purposes), and as obviously there is no empirical method for such a separation, this separation can only be done theoretically using mathematical models and strictly defined concepts and rules, which may differ strongly between different modelling approaches (Emmans, 1994). Despite this, it is interesting that these arbitrary concepts have been widely adopted in livestock research, and they are even applied in practical livestock production. For example, similarly to 'metabolisable energy', feed producers are sometimes providing information on the concept called the 'net energy' content of the feed, which is supposed to indicate that fraction of the combustion energy that is utilizable for growth and maintenance only, excluding all 'inefficiencies' occurring within the animal (Noblet *et al.*, 1999). Again, the feasibility of such arbitrary information is questionable, especially when applied for predictions of performance of single animals, which are expected to have differences in their processes of energy flow and energy partitioning (Emmans and Kyriazakis, 2001; Emmans, 1994).

As previously, we can formally state the principle of energy conservation during growth. The rate of gain in chemical energy (E) of a growing animal can be expressed as a balance between rates of energy input from feed and energy output in waste and heat:

$$(chemical\ energy\ of\ feed) = \frac{dE}{dt} + (chemical\ energy\ of\ waste) + (metabolic\ heat\ loss) \quad (3)$$

In a growing animal the rate of energy gain is positive.

2.3 *Biological constraints*

As discussed above, the growth is necessarily constrained by the rate of input of resources, which in the case of animals are high-energy compounds (together with some minerals), obtained from feed. In intensive livestock production, there are usually no limitations in the potential supply of energy (i.e., monogastric animals are allowed to eat *ad libitum* a high quality feed), although there are some exceptions (Sandilands *et al.*, 2006). Such exceptions include the restricted feeding of the parent birds of meat chickens, and this is discussed in more detail in section 4.1. However, in general as a result of this 'unlimited' food supply, the input of resources needed for growth under typical commercial conditions of livestock production can be considered to be mainly constrained only by the animal itself.

The most obvious internal factor limiting the feed intake of an animal is its size (Emmans and Kyriazakis, 1995). It is quite clear that a small animal can eat less than a large animal, and, therefore, the feed intake capacity of a young growing animal is initially low but then continuously increases (Whittemore *et al.*, 2003b). However, although the size is the main limitation of feed intake, there are other factors causing differences between animals of the same age or same size. For example the appetite of an animal can vary, there can be effects of social interactions and behavioural patterns on animals in a herd or flock (e.g., the most aggressive animals might have better access to feed), health conditions of an animal might affect its capacity to eat, and so on.

All these internal factors affecting the feed intake (and ultimately the growth) of an animal can be considered to be part of phenotypic variation between individuals. The phenotype of an animal is defined as the composite of observable characteristics or traits, and results from the expression of genes as well as the influence of environmental factors and the interactions between the two. Although this is a generally accepted definition, it would be useful to emphasize here the fundamental difference between the phenotype and genotype, as in livestock research there often seems to be confusion between these two concepts. The genotype of an animal is defined as the inherited instructions the animal carries within its genome. Therefore, the genotype cannot be actually specified without examining the DNA sequence itself. As a result, modelling of growth of an animal must always be based on its phenotype (observable traits) which includes both the genetic (inherited) component and current and past effects of environment. It should always be kept in mind that these components cannot be separated by observation, and, therefore, the environmental component (no matter if it is a known consequence of certain environmental conditions, or 'built in' the modelled trait) must always be present in the models and their parameters.

Chapter 13 In: Paul J. Moughan and Wouter H. Hendriks, ed. Feed Evaluation Science. Wageningen: Wageningen Academic Publishers, 2018

3. Principles for modelling growth in livestock animals and populations

In this section we present principles and approaches for the quantitative modelling of livestock growth under general conditions where there is a sigmoidal increase in animal size. These principles and approaches comply with the general physical, chemical and biological principles presented in section 2.

3.1. *Common variables for describing growth*

Following the principles described above, an animal is in a state of growth when it undergoes a period of systematic net increase in body mass. Here, we focus on the growth of livestock animals from birth to maturity or slaughter, whichever occurs first. A typical pattern of increasing body weight during a period of growth is the top curve shown in Figure 2.

As a first approach to describing growth, it is common to focus on total live body weight (BW, kg), which comprises empty body weight (eBW, kg) and fill of the digestive and urinary tracts. Measurements of BW are noisy, even under tightly-controlled growth conditions, because there is random variation in the animal's gut and bladder fill as well as measurement error (e.g., in the time and scale of reading). For common lines of pigs, gut and bladder fill is on average 5% of empty body weight at any age (t) of the animal (Emmans and Kyriazakis, 1995; Whittemore *et al.*, 2003a):

$$eBW(t) = 0.95BW(t) \quad (4)$$

More elaborate descriptions of body mass will include specification of mass content per tissue component, such as mass of protein and lipid. We will consider both descriptions later.

3.2. Range of growth conditions

We recall the inputs and outputs (section 2), the positive net balance of which leads to a state of growth (Figure 1). This net balance reflects the resources that are available for growth; it can have different levels depending on the influence of the animal and external conditions on the inputs and outputs. Inputs are controlled by the available diet and the animal's appetite (influenced by size and health status, surrounding temperature and sanitation, and social interaction). The outputs depend on animal functions involving release of waste and heat.

The theory and models presented in this chapter apply to a given animal breed or species, from birth to maturity, and over a wide range of growth conditions (Figure 3A). The figure shows a hypothetical probability distribution of animal size (at given age) across the whole range of growth conditions; the mean of the distribution represents growth in an average commercial farm. The growth conditions are genetically bounded by the survival (and reproduction) of the animal, and include conditions typical of breeding stations and experimental settings, where phenotypical traits are expected to be closer to genetically determined traits, right through all conditions in commercial farms where animal performance decreases as a result of increasing limitation in availability of resources for growth (Black *et al.*, 2001). The limitation may be in the amount and quality of feed intake, or in how much of the resource intake is available for

Chapter 13 In: Paul J. Moughan and Wouter H. Hendriks, ed. Feed Evaluation Science. Wageningen: Wageningen Academic Publishers, 2018

growth, which is determined by primary use of resources for animal functions such as production of metabolic heat, and immune response triggered by exposure to pathogens.

When the growth conditions are stable, in the sense that the environmental factors are kept relatively constant over time, we expect the animals to exhibit a sigmoidal pattern of growth. There is evidence that a sigmoidal pattern of increase in body weight and in content of tissues such as protein and lipid, is robust across breeds (Kyriazakis *et al.*, 1994) and species (Emmans and Oldham, 1988), (Figure 2). In practice, there is usually a significant level of influence from random disturbance (in relation to tightly-controlled conditions), but a sigmoidal pattern can still be discerned in an animal's increasing size if the magnitude of disturbance is sufficiently low. Growth models in a basic form apply to regimens where growth is sigmoidal (or at least where there is a simple pattern of increasing size). In breeding stations and in commercial farms, the growth conditions change from birth to slaughter according to a predefined schedule. If there is no significant change in growth pattern as a result of these changes in conditions, a sigmoidal growth model also applies to growth under these conditions. Otherwise, provided that conditions are kept constant within consecutive periods of time, we expect growth to be sigmoidal within each such period (up to possible brief intervals of animal adaptation between periods); hence, a piecewise model made of several sub-models applies, with each sub-model describing sigmoidal growth (with specific parameters) in each period with constant conditions. While linear and sigmoidal growth patterns may not be discernible in growth data over short periods, sigmoidal growth models are necessary for extrapolation beyond these periods. Such a piecewise model can apply to farms and to other situations where there is one or more points of change in growth conditions. In farms, the scheduled changes (e.g., in diet and in temperature) usually cause a shift to a lower rate of growth. Other types of change in growth conditions (e.g. from more to less restricted feeding, bottom curve in Figure 2, (Stamataris *et al.*, 1991)) led to a shift to a higher rate of growth. If both periods of growth are approximately sigmoidal, such that the piecewise model applies, the long-term pattern of growth is not discernible from that of stable conditions (Figure 3B).

We can regard the range of conditions spanning from average farm to breeding stations (Figure 3), which includes mild to moderate limitations to growth, as normal growth conditions. The usefulness of this idea is in allowing us to consider a minimum range of conditions under which body composition (e.g., relative protein and lipid content), conforms to expectation (Emmans and Kyriazakis, 1997; Whittemore *et al.*, 1988) and thus complies with production requirements.

3.3. Single- variable model of growth

In deriving a model of animal growth under relatively stable conditions, we focus first on a single state variable animal; that is we attempt to describe the net increase in body weight (1) as a process governed by BW alone or by body weight and age (t). We do not start by assuming sigmoidal growth but, rather, we will derive the conditions for it to occur.

As illustrated in Figure 2, growth can appear to be linear over a limited period of time. We can extrapolate by assuming that the net rate of body weight gain (1) is constant since birth:

$$\frac{dBW}{dt} = b \tag{5}$$

Chapter 13 In: Paul J. Moughan and Wouter H. Hendriks, ed. Feed Evaluation Science. Wageningen: Wageningen Academic Publishers, 2018

which, using $BW(0)$ for body weight at birth, leads to linear growth:

$$BW(t) = BW(0) + bt \quad (6)$$

However, based on the expectation that an animal should (at least initially) grow faster as it becomes bigger, we may assume that the rate of growth is proportional to the animal size:

$$\frac{dBW}{dt} = bBW \quad (7)$$

which gives an exponential growth curve,

$$BW(t) = BW(0)\exp(bt) \quad (8)$$

Two features appear in models (5) and (7). First, they have two parameters, the initial size *BW(0)* and the rate parameter *b*, that set a scale for the dependent and independent variables, respectively. However, if we are given or can measure the initial size, we can say these models have a single parameter. Secondly, and most importantly, growth in either model never stops as the animal ages: it occurs either at a constant rate in (5), or at an ever-increasing rate in (7), either of which leads to unbounded growth (Figure 4).

Clearly, we need a model of bounded growth, as animals slow down their growth rate and eventually attain a limit size, mature size (BW_m, kg), during their life span. As discussed in sections 2.3 and 3.2, the specific size a mature animal attains is a phenotype. For example, in pigs of a given breed, mature size was estimated for animals growing past slaughter age, and was found to be significantly larger than the typical size at slaughter (Strathe *et al.*, 2010). Moreover, there is no evidence for a specific age at which growth starts to slow down or ceases altogether; this implies that animals reach maturity in an asymptotic manner (i.e. through a gradual and continuous decline in the growth rate since a time after birth) rather than through a sudden switch to zero growth. Two models of bounded growth can be derived from (5) or (7) by assuming that the rate of growth is compounded with an exponentially-declining factor since birth (*a exp(-bt)*, where *a* is an additional constant); these assumptions give the growth rate

$$\frac{dBW}{dt} = bae^{-bt} \quad (9)$$

which leads to a monomolecular growth model (after choosing $a=BW_m - BW(0)$), also known as law of diminishing increments:

$$BW(t) = BW_m - [BW_m - BW(0)]e^{-bt} \quad (10)$$

and the growth rate

$$\frac{dBW}{dt} = bae^{-bt}BW \quad (11)$$

which gives the so-called Gompertz growth model (Winsor, 1932):

$$BW(t) = BW_m\exp(-a\exp(-bt)) \quad (12)$$

where $a = ln(BW_m/BW(0))$ measures the degree of maturity at birth.

Figure 4 compares body weight, and its rate of change, among the models with bounded growth (monomolecular and Gompertz) and against the models with unbounded growth (linear and exponential). Three points are worth making. First, bounded growth models require two

parameters, unlike unbounded growth models which have one parameter: the mature size BW_m and the parameter rate b, which in this case is the rate of approach to maturity. Second, the rates of change (7) and (9) are net rates, i.e. the balance between input and output in (1), but are often written as a difference between positive and negative terms; respectively,

$$\frac{dBW}{dt} = b[BW_m - BW] \tag{13}$$

and

$$\frac{dBW}{dt} = b[\ln(BW_m) - \ln(BW)]BW \tag{14}$$

Do the terms in (13) and (14) represent the mass input (feed intake) and output (waste and maintenance) flows in (1)? Probably not; while their difference might match net flow data, the individual flows are likely to be more complicated functions of the animal's state variables. While it is straightforward to measure net changes in body weight, it is more difficult to measure mass input and output rates and thus to test specific models for these flows even when we know their net difference. Third, while we have ruled out unbounded models as plausible growth models, we are still left with the task of identifying which bounded-growth model is adequate for describing animal growth. Again, we can generally rule out the monomolecular curve for this purpose as it has a concave shape while the Gompertz curve has a sigmoidal shape (Figure 4A). These correspond, respectively, to a growth rate that declines since birth or one that reaches a maximum after birth (Figure 4B), and evidence overwhelmingly supports that new-born animals have not yet achieved their peak in growth. This point of maximum growth, or inflection point, occurs in the Gompertz model when the animal reaches about 37% of its mature size, at an age determined by the rate parameter and the degree of maturity at birth:

$$BW_i = \frac{K}{e}, \;\; t_i = \frac{1}{b}\ln(a) \tag{15}$$

where e ≈ 2.71. There are sigmoidal growth models with other inflection points, such as the logistic model (Robertson, 1908), which has maximum growth at 50% of mature size, or the Richard's model (Richards, 1959), which has an adjustable inflection point due to it having a third (shape) parameter. However, it is found that the Gompertz model fits a variety of animal growth data remarkably well. Figure 5 gives an example where we fitted several growth models to the live weight of one growing broiler. Other comparative studies (e.g., Wellock *et al.* (2004)), have shown the Gompertz model to fit growth data as well as sigmoidal functions with flexible inflection points and better than other two-parameter sigmoidal curves. As the extra accuracy from using shape parameters has a cost in terms of reduced interpretability and ability to estimate parameters, they concluded that the Gompertz model is a suitable descriptor of animal growth. Thereafter we adopt this model as a practical tool for describing growth, which is thus characterised by the rate b and the mature size BW_m. One limitation of the model, however, is that it relies on the point of maximum growth not varying among animals or across generations (for a given mature size), while there have been suggestions it could be changing due to selection and breeding (Knap, 2000b).

Chapter 13 In: Paul J. Moughan and Wouter H. Hendriks, ed. Feed Evaluation Science. Wageningen: Wageningen Academic Publishers, 2018

3.4. Is mature size a useful concept?

There are possible criticisms of the concept of mature size because the growth of most livestock is only partially observed, because animals usually are slaughtered prior to maturity. In pigs, for example, it has been estimated that the mature size BW_m can be as great as three or four times the typical size at slaughter (Strathe *et al.*, 2010). One plausible criticism is that we may not be able to accurately estimate BW_m. However, we often have body weight measurements over an age period where there is significant change in growth rate and such detail may suffice to allow this parameter to be estimated (i.e. to allow statistical identification of unique parameter values for which the model fits the observations). The uncertainty in the estimation, however, is larger when the span of observations is small.

A second possible criticism, concerns the usefulness of estimating BW_m when it is possible to do so, because estimating the animal's age at a given slaughter size is often of greater practical interest. Moreover, it would not be possible to verify the estimation from the measured size at slaughter. We note, however, that the choice of weight/age for slaughter is arbitrary. Therefore, provided that the parameters of the growth curve (or curves, for multivariable models) have clear biological meaning, as the Gompertz parameters do, then they provide a way of characterising and identifying different kinds of pigs or other species of animal according to their estimated mature size; therefore, providing some guidance on typical age or size at slaughter among breeds of animals (Ferguson *et al.*, 1994). Note, that to be able to compare breeds or genotypes, we would generally need to fit data from breeding stations or experiments for each breed (Figure 3). In the case of multivariable models (see below), we may be more restricted or totally unable to measure the animal component (e.g., protein mass) we are estimating the growth parameters of. Estimation of mature size is at least as useful in this case, for the same reasons as for body weight. If the component is never observed, however, there is greater uncertainty in the estimated mature size.

3.5. Multivariable, energy and mass flow models

So far, we have described growth in terms of body mass alone via single-variable models that are simple and easy to implement and, as discussed in section 3.6, are helpful for comparative characterisation of growth among breeds and species. However, growth models with multiple state variables are necessary to predict the changing body composition during growth. Moreover, a more robust description of growth must account for heat loss as this limits how much growth is possible according to body size and composition. As already discussed in Section 2, the chemical transformations and heat losses involved require a computation of the energy flow in addition to that of the mass flow governing growth.

A commonly used characterisation of the composition of empty body mass is in terms of: 1) protein, 2) lipid, 3) an aggregate of minerals, mostly in bone (ash), and 4) water (Armsby and Moulton, 1925). The relative proportions of these components change during growth. For example, animals growing under 'normal' conditions preferentially gain protein and are leaner at earlier growth stages, while the proportion of lipid generally increases nearer maturity (Emmans and Kyriazakis, 1997; Whittemore *et al.*, 1988). As explained above, the growth in protein and lipid, unlike the growth in ash and water, involves the storage of chemical energy in the animal body through a flow and conversion of energy from the feed. These energy flows

are controlled by broadly-defined processes (Figure 6): energy intake in the form of chemical (combustion) energy in feed, partitioning of 'metabolisable' energy (i.e., that which is not lost in faeces, urine, or in enteric fermentation as methane, hydrogen, and heat of fermentation) among maintenance functions (leading to heat loss) and deposition of protein and lipid tissues, which together with water and mineral intake results in growth of body mass over time.

Growth is subject to the conservation of measurable physical quantities: body mass, measured as body weight (*BW*), and energy (*E*) (Figure 1), according to the conservation laws (1) and (3). These laws constrain the dynamics of the body components' mass content (kg): protein (Pr), lipid (L), ash (A), and water (W). Considering daily flows, and specifically, daily metabolisable energy intake (*MEI*, MJ/day), daily metabolic heat production (*H*, MJ/day), and daily changes in empty body weight, protein, lipid, ash, and water (*DeBW*, *DPr*, *DL*, *DA*, *DW*, kg), the following balances hold:

$$MEI = H + g_P DPr + g_L DL \tag{16}$$

$$DeBW = DPr + DL + DA + DW \tag{17}$$

where g_P and g_L are the combustible energy content (MJ/kg) of the deposited tissues. These constraints hold independently of the model of growth dynamics to be specified.

To describe animal growth, we make similar assumptions for each body component as those made above for the total body mass (i.e., Equation 12). Here, we follow the accepted principle that lipid-free dry matter (protein and ash) is the best indicator of progress towards maturity, as it forms the primary structure of the body, has essentially constant composition (i.e., a constant ratio *A:P*, see below), and holds a direct relationship to the metabolic processes (Schmidt-Nielsen, 1984). Based on this principle, several authors have favoured the use of the Gompertz curve for describing growth of protein (or, protein and ash) in pigs (Emmans, 1984) and in chickens (Emmans and Fisher, 1986). Successive mathematical models of livestock growth have adopted the same practice for both protein and lipid growth (Emmans and Kyriazakis, 1997; Emmans and Oldham, 1988; Ferguson *et al.*, 1994; Wellock *et al.*, 2003a). We note that as lipid is not primarily a structural tissue and grows more variably among animals, the assumption is less robust for lipid than for protein, although it is still plausible under 'normal' conditions. Therefore, we assume that protein and lipid are described by Gompertz functions of age since birth; expressed in terms of degrees of maturity, these read:

$$\frac{Pr(t)}{Pr_m} = \exp(-a_{Pr}\exp(-bt)) \tag{18}$$

$$\frac{L(t)}{L_m} = \exp(-a_L\exp(-bt)) \tag{19}$$

where the rate parameter b is assumed to be the same for both tissues based on empirical evidence (e.g., Kyriazakis (1989) and Ferguson and Kyriazis (2003)), Pr_m and L_m are the maturity mass content parameters, and $a_{Pr} = \ln(Pr_m/Pr(0))$ and $a_L = \ln(L_m/L(0))$specify log-degree of maturity at birth.

A common alternative way of formulating lipid mass content (Emmans and Oldham, 1988; Moughan *et al.*, 1990) that is equivalent to directly assuming Gompertz dynamics, is to assume that lipid holds an allometric relationship (Huxley, 1932) to protein at all times during growth:

$$\frac{L(t)}{Lm} = \left(\frac{Pr(t)}{Prm}\right)^{b_{LP}} \quad (20)$$

where parameter b_{LP} was related empirically to the maturity sizes in Emmans (1997). The equivalence follows by noting, from Equations (18)-(19), that $(L(t)/L_m)^{(1/a_L)} = (Pr(t)/P_m)^{(1/a_{Pr})}$; hence, by taking the power a_L of this equation we immediately obtain Equation (20). Moreover, as Equation (20) is assumed to hold at all times, we can take $t = 0$ in Equation (20) and obtain an exact expression for b_{LP}:

$$b_{LP} = \ln\left(\frac{Lm}{L(0)}\right) / \ln\left(\frac{Prm}{Pr(0)}\right) = \frac{a_L}{a_{Pr}} \quad (21)$$

which, therefore, does not necessitate empirical determination. This follows from the fact that as $L(t)$ has two independent parameters, L_m and b, these must suffice to determine b_{LP}.

To complete the growth dynamics of body components, we note that the mass content of ash and water relate empirically to protein mass content, under broad conditions, through isometric and allometric relationships (de Lange *et al.*, 2003; Kyriazakis and Whittemore, 2005):

$$\frac{A(t)}{A_m} = \frac{Pr(t)}{Pr_m} \quad (22)$$

$$\frac{W(t)}{W_m} = \left(\frac{Pr(t)}{Pr_m}\right)^{b_{WP}} \quad (23)$$

where $A_m/Pr_m=0.20$, $b_{WP}=0.885$, and $W_m/P_m=3.04$ for growing pigs (Kyriazakis and Whittemore, 2005). Note that the water content should be independent of the lipid content as lipid does not contain water. While it is not viable to collect longitudinal data on most components of a given growing animal, there is evidence that the growth of bone (the main component of ash) follows a Gompertz curve (e.g., Montes *et al.* (2005)).

The remaining elements to be defined in this model are the daily *MEI* and the metabolic heat production rate (H) introduced in the energy balance Equation (16). One approach to defining *MEI* is to input suitable estimates for a given diet, with the caveats already discussed in section 2.3. On the other hand, definition of daily metabolic heat during growth requires identification of a suitable relationship to the animal's state variables in the model. Empirically-based relationships between M and growing body weight (H = constant BW^b) have been found for domestic birds and pigs (Berman and Snapir, 1965; Brown and Mount, 1982; Noblet *et al.*, 1999); while other authors have favoured relationships involving body composition, such as H = constant Pr (Emmans, 1994; Noblet *et al.*, 1999). This is a topic of ongoing research in the development of predictive animal performance models.

The set of state variables, Pr, L, A, and W, specified by Equations (18), (19), (22), (23) specifies the mass composition of a growing animal provided that we know appropriate values for the parameters involved. While literature sources may provide some insight, joint statistical estimation of the parameters to suitable empirical data (by constraining the state variables to obey the conservation laws in Equations (16) and (17)) is essential for mutual consistency of parameter values and consistency with the data, the growth model, and the conservation laws. The study by Strathe *et al.* (2012) is an example of statistical fitting of a related multi-variable model to pig growth data: it estimates the breed characteristics b, P_m and L_m and heat production parameters. In conclusion, multivariable-models such as the one we have derived

can be parameterised using suitable empirical data, with a view to predict performance under a range of growth conditions.

3.6. Phenotypical characterisation of individuals and phenotypical landscape of populations

In this section we take a step further by using the models described above to characterise differences in performance among individual animals, and the range of such performances within a group of animals. Examining growth across individuals often reveals that individual patterns are not smooth due to randomness in the environment, as well as measurement error and data incompleteness. While this type of variation can explain some differences in trait observations among animals and increased uncertainty in parameter estimates, we do not examine it here (see for example Reed *et al.* (2016)). Growth across individuals can also reveal systematic variation in performance among animals that producers hope to manage to an advantage. It has been suggested (Emmans and Oldham, 1988; Ferguson *et al.*, 1994) that such phenotypical differences in growth pattern, which must result from differences in genetic characteristics and/or differences in growth conditions (Figure 3), can be characterised by differences in the estimated parameters of the growth model. Hence, the parameters of the Gompertz functions for protein and lipid growth (sec. 3.5) or for live weight (sec. 3.3) would offer a practical means of characterising these phenotypes (Ferguson *et al.*, 1994). This characterisation relies on the assumption that a single growth model, e.g., the Gompertz, is equally suitable for describing all individuals or groups under phenotypical comparison. This implies, in particular, that the growth pattern must be sigmoidal and thus that growth conditions must be suitable (section 3.2). Since the Gompertz model parameters have biological meaning, they can also be interpreted as phenotypes; however, as they may not be directly observable (e.g., the mature size, see section 3.4), they are theoretical phenotypes. Here, we adopt the above approach as a practical means of characterising observed growth among animals and thus of classifying them according to a desired performance.

As livestock are reared in groups and individual animals differ in their performance, it is important to quantify and predict performance (e.g., protein mass content at a given live weight, or live weight at a given age) at population or breed level. However, as prediction based on an average animal is not informative when there is significant or skewed phenotypical variation, population approaches that quantify variation as well as average performance within a herd or breed offer a more informed basis for deciding which management and feeding strategies optimise resource use and herd performance. Furthermore, such population approaches can be used to identify new phenotypes, from growth observed across individuals, or to predict the growth of newly-identified phenotypes (Ferguson *et al.*, 1997; Knap, 2000a).

The typical population approach taken in the literature (Ferguson *et al.*, 1997; Knap, 2000a; Knap *et al.*, 2003; Pomar *et al.*, 2003; Symeou *et al.*, 2016) is to assume and simulate from a plausible population distribution of theoretical phenotype parameters characterising individual performance, such as the Gompertz parameters for protein and lipid mass content, as wells as parameters associated with metabolic heat production. By simulating growth multiple times with parameters sampled from the assumed distribution, one can estimate a population distribution of traits such as protein mass content or live weight (Ferguson *et al.*, 1997; Knap *et al.*, 2003).

A data-based approach to the same problem consists of estimating from data, rather than assuming, the population distribution of the theoretical parameters characterising performance. The rationale in such an approach is that we do not know these distributions. This is especially so as there is uncertainty in the point estimates of parameters that would inform the construction of assumed distributions, and even more so for theoretical phenotypes that are not testable against direct observation. In the context of Bayesian statistical inference (Gelman *et al.*, 2013; Sivia and Skilling, 2006), this approach is known as estimating the posterior distribution of the parameters given the information in the data and the assumptions of the growth model. Here we give an example application to modelling live weight growth of pigs and chicken (unpublished data), where we have estimated the posterior distribution of the model parameters by fitting the model (12) to data, and subsequently generated a posterior distribution of predicted live weight performance by simulating the model from the data-based parameter distribution. Correlation among model parameters (Vautier *et al.*, 2013) is automatically incorporated in this distribution by using likelihood-free, simulation-based parameter estimation that relies on weaker distributional assumptions (Beaumont, 2010). Figure 7 shows the predicted distributions of live weight of growing male pigs from 60 to 360 days (fitting the model to data from 60 to 180 days), for a selected individual (left) and for a population (right). Figure 8 shows similar results for two groups of growing broilers from two distinct strains. The usefulness of this approach lies in allowing a distributional phenotypical characterisation of groups that is fully data-based (i.e. relatively free from distributional assumptions). Based on this characterisation it is possible to identify the level of phenotypical uniformity or heterogeneity within groups. It is also possible to predict breed distributional performance for multiple purposes, including the prediction of future performance of a cohort under specified conditions, and prediction of offspring distributional performance from that of the parents.

4. Growth under different degrees of limitation in the availability of resources

The examples presented above show the growth patterns of an animal under conditions where no severe limitations in availability of resources for growth occur. However, such conditions are not always met, even in high-standard livestock production systems, and especially when the animals are grown in 'natural' or 'semi-natural' outdoor conditions. Under such conditions, the rate of growth or the overall growth pattern is expected to be altered.

Despite the established fundamental principles of modelling growth, it appears to be extremely difficult to quantitatively predict the exact response in the magnitude and nature of growth (for example in terms of changes in body composition) to changes in different kinds of environmental constraints, including changes in the limitation of resources for growth. In this section, some attempts aiming to solve this problem using modelling approaches are discussed. It seems quite clear that currently there are no 'universally applicable' methods or models to predict the growth of an animal across conditions where different levels of limitations apply. However, we try to present examples of different responses to different kinds of constraints (and recovery after the conditions are improved) and put these into the context of the fundamental principles of growth presented earlier, while also showing some results from the literature demonstrating the multitude of these responses. As a result, this section also demonstrates some of the main challenges for the future development of animal growth models.

4.1. *Limitations in energy provision*

One of the conditions of energy limitation that is generally (and intentionally) applied in practical livestock production is in the feeding of parent birds of broilers. While standard broilers have *ad libitum* access to feed and in general are encouraged to achieve high feed intakes, the parent birds are grown under strictly limited energy supply. Therefore, the parent and broiler birds of the same breed provide an interesting opportunity for comparing the effects of environmental constraints in genetically similar animals.

Here we use the most recent publically available performance objectives for one of the most common broiler breeds, namely Ross 308 (Aviagen, 2011; 2014b), to compare the energy intake and growth of parent and broiler birds. According to these objectives, if the male broiler bird would be allowed to grow 70 days with *ad libitum* feed intake, its total energy intake would be expected to be about 40 000 kcal (i.e., on average 570 kcal/d). In contrast, the cumulative energy intake of the male parent bird of the same age would be restricted to 11 000 kcal, or 158 kcal/d on average. When looking at single high-energy compounds in the diet, the difference is even more striking. For example, following the nutritional guidelines (Aviagen, 2014a; 2016), during the same 70 days period the intake of lysine, one of the essential amino acids necessary for growth, would be in total about 0.12 kg for the *ad libitum* feed intake, while under restricted feeding, it would be as low as 0.02 kg.

When comparing the effect of these restrictions on growth, the difference between the *ad libitum* and restricted feeding is dramatic (Figure 9). It can be seen that under the limitation, the 70 days old parent bird has reached only 30% of the body weight of the *ad libitum* fed broiler bird of the same age. It is interesting, however, that the growth curves for these two different birds seem to follow a similar pattern (resembling the Gompertz function), only the level of the final body weight seems to be much different. This picture conforms to the framework described in Figure 3.

Although the effect of energy limitations on growth is well known and applied for practical purposes, there is no uniformity in how it is described in mechanistic growth models. Following the fundamental principle of energy conservation explained above, it is necessary that when the (metabolisable) energy intake is reduced compared to a 'standard' condition, one or several of the following components must be also reduced: 1) protein growth, 2) lipid growth, or 3) metabolic heat production. The relative reduction in these components is often modelled based on a principle of 'priorities' of different metabolic processes, expecting that the relative proportions of the energy portioned to different components changes as the total input changes (Coop and Kyriazakis, 1999; Doeschl-Wilson *et al.*, 2008). A common expectation is that of these three components, the metabolic heat production is the prioritised one, while lipid growth is considered as a 'reserve' of energy and, therefore, always reduced when the energy intake is decreased.

As an example of modelling energy partitioning under a range of conditions of differing levels of limitation in energy provision, we present an approach used in the InraPorc model (van Milgen *et al.*, 2008), which is one of the most detailed metabolic models currently used in monogastric livestock production. In that model the starting point in energy partitioning is 'maintenance', i.e., energy used for basic metabolic functions (and eventually released as heat)

(Figure 6). The model specifies a certain 'maintenance energy requirement', and if the available 'net' energy intake falls below this point, the energy deposition for protein and lipid growth equals zero (see Figure 2 in van Milgen *et al.* (2008)). When the energy intake increases above this point, the protein and lipid deposition also increase. In conditions of low energy supply, most of the available energy (remaining after the 'maintenance requirements' have been fulfilled) is used for protein growth at the cost of lipid deposition. When the energy supply increases, the proportion of the available energy used for lipid deposition also increases. Finally, when there is sufficient energy available for protein deposition to reach a maximum level (determined by the Gompertz curve specific for the phenotype), all the additional energy intake is used for lipid deposition.

There are several modelling approaches (differing in technical detail) for explaining in quantitative terms this process of energy partitioning under restricted energy intake that are based on the common idea of prioritisation. Such approaches have been reviewed in Kyriazakis (1989) and Emmans and Kyriazakis (1997), where it was shown that they are all based on the assumption that protein growth is prioritised over lipid growth (similarly to the example above), but in the different models this priority is set to be constrained in different ways. This can be described for example by the concepts of either minimum lipid:protein gain ratio, minimum marginal lipid:protein gain ratio, or more detailed functions including the effect of other factors such as feed composition (Kyriazakis and Emmans, 1992a; b). Although such approaches present (theoretical) quantitative solutions for modelling the consequences of energy limitation on growth, it should be kept in mind that these kinds of model responses are based on some arbitrary assumptions based on empiricism. The parameters describing these quantitative responses are assumed to be constant, but are likely to change depending on the type of animal and various environmental conditions. Therefore, modelling mechanistically the energy partitioning under constrained conditions remains a major challenge in the research currently carried out to predict the growth of animals. The challenge is even greater when additional functions need to be considered, such as for example the need for the animal to cope with pathogens whilst it is given access to limited energy; this problem is considered further in 4.3.

4.2. *Limitation in mineral provision*

Similarly to the energy deficiency, limitations in the intake of certain minerals are also known to affect growth. Here the key questions are the following: What is the critical level of intake of a specific mineral below which growth is reduced? What is the magnitude of growth reduction at a given level of limitation in mineral provision? And finally, how can the models be used to predict such effects on growth? To answer the last question, various approaches for quantifying the relationship of the content of certain minerals in the body and other body components (most notably protein) have been developed. These approaches are discussed in more detail below.

As demonstrated in section 3.5, there is a common, simplified approach to modelling the growth of certain components of the animal body. This approach uses some pre-defined relationships between the mass of the unknown components and the mass of those components the growth of which can be more easily measured or can be more reliably predicted. The relationships between the masses of different body components can be based on strictly

functional interactions, or they can be mainly empirical correlations without a functional foundation. For example, it can be expected that the composition of animal cells (in either skeletal muscles or internal organs) remains more or less constant, to allow the optimal cellular processes. Therefore, as the animal grows, the cells remain similar in terms of their content of, for example, protein, lipid, water and certain minerals; only the number of these cells increases. Therefore, the relative proportions of these compounds within these specific tissues can be expected to remain unchanged. However, this relationship does not necessarily hold when the whole animal is considered, as the relative proportion of different types of tissues is likely to change (e.g. the proportion of fat cells increases as the animal gets more mature). Therefore, in the case of the entire body of the animal, the relationships between different compounds are probably less functional, but rather based more or less on the individual growth of different organs. However, even at the whole-animal level a correlation basis for a relationship can still be seen: an animal with high muscle mass (and high protein content) is likely to also have high bone mass (and high mineral content) (c.f. Equation (23)).

Another question when modelling the mass of different compounds is whether the proportions of these compounds remain the same during the lifespan of the animal or not. In animal research, a constant, unchanged relative proportion of two or more components is sometimes called (somewhat misleadingly) isometric relationships. In contrast, a relationship that allows (a specific form of) change in relative proportions of components as the animal grows is called an allometric relationship (see Section 3.5; Huxley (1932)). Obviously, if the assumption of a constant proportion would be universally valid, that would make predictions of the body composition and growth much easier: measuring the mass (or increase of mass) of one compound within the body would make it possible to estimate the mass (or growth) of other compounds at any stage of the growth cycle. Unfortunately, such a relationship very rarely holds. In reality, the 'shape' of the animal also changes, together with its size. Therefore, the relative proportions of different tissues (e.g., skeletal muscles, bones, internal organs, fat deposit) are generally not constant, and so it is understandable that the proportion of different components does not remain constant either. Nevertheless, allometric relationships such as (24) offer a first approach to capturing non-constant relative proportions.

In cases where it is valid, the assumption of constant relationships between relative proportions of mineral and protein components can be very useful. For example, the isometric relationship (23) between body mineral (ash) and protein content is expected to hold under conditions not severely limiting in mineral provision. If a similar relationship would hold under broader conditions for specific minerals such as phosphorous or calcium, it would allow prediction of the effect of mineral deficiencies on the growth of animals. Attempts to do so using modelling have been made (e.g., Symeou *et al.* (2014a) and Symeou *et al.* (2014b)); applying the principle of mass conservation, it would be possible to predict the changes in retention of a mineral under conditions of deficiency, and thereafter, the principle of isometric relationship would allow direct prediction of the overall growth of the animal. Again, unfortunately reality is not as simple as this.

In another modelling attempt, Letourneau-Montminy *et al.* (2015) present a nice demonstration of the relationship between body mineral (ash) and protein content in pigs by plotting data from several experiments with or without mineral deficits (see Figure 1 in Letourneau-Montminy *et al.* (2015)). It can be seen that without the deficit, the protein:mineral ratio remains approximately constant across different experiments and sizes of animal. In contrast, under

Chapter 13 In: Paul J. Moughan and Wouter H. Hendriks, ed. Feed Evaluation Science. Wageningen: Wageningen Academic Publishers, 2018

conditions of deficit, the mineral content drops below the predicted level in relation to the protein content. A similar conclusion can be reached when reanalysing the results from a series of recent extensive experiments defining the phosphorus requirements of pigs of various ages (Zhai and Adeola, 2013a; b; 2015). The results generally show that although the overall growth of the pigs is reduced after the phosphorus intake falls below a certain critical level, this reduction remains relatively smaller than the relative reduction in the observed phosphorus intake (and estimated retention) (Figure 10).

These examples demonstrate the principle that although empirically observed trends can be useful in modelling animal growth under certain conditions, such as 'average' commercial settings, under severe mineral limitation such rules may no longer apply satisfactorily. For example, growth patterns that show constrained growth as a result of phosphorus deficiency, are caused by the effect of the deficiency on animal functions. Although phosphorus is an essential element in various metabolic processes, under unconstrained supply, a clear majority of the animal phosphorus content is located in the bones as part of structural materials or as 'reserve'. Under conditions of deficiency, these reserves are mobilized to be used in metabolism, and as a result, the bone phosphorus content is reduced, and the overall body protein:phosphorus ratio altered. Understanding this relatively complicated process is needed to quantify the effect of such deficiencies on animal growth, and this brings in additional challenges for modelling growth under limiting conditions.

4.3. *Growth-limiting health conditions*

A special case to consider is the growth of animals during exposure to health challenges, such as pathogens. As expected, the growth of these animals is less than that of their healthy counterparts. Health challenges are associated with increases in the maintenance requirements of animals, due to pathogen associated functions, including an immune response to pathogens and the resources required for repair of tissues that have been damaged (Kyriazakis and Houdijk, 2007). In theory, this could be counteracted through increases in the food intake of the animal, so that its growth would not be penalised by the health challenges.

In reality of course, this is not what happens; challenged animals actually have a decreased feed intake and a substantially reduced growth compared to healthy ones. This has been considered a paradox (Kyriazakis, 2014). Laurenson *et al.* (2011) have suggested this reduction in food intake during health challenges, frequently called pathogen-induced anorexia, can arise as a consequence of one of two mechanisms. Wellock *et al.* (2003b) suggested that the reduction in food intake is a consequence of a reduction in the intrinsic growth rate of the animals (mechanism 1); the implication of this is that the reduction in food intake may be modelled as a consequence of the reduction in growth. The suggestion further implies that an animals' intrinsic growth capability changes, for example, in a manner akin to the gene expression alterations seen with epigenetic programming (Burdge *et al.*, 2007). Sandberg *et al.* (2006), on the other hand, have suggested that anorexia could be modelled as a direct reduction in the food intake of the challenged animals (mechanism 2), which may be due to inappetence caused by immune response components such as cytokines. These authors have used this approach to model the time trend of food intake during the course of infection, mainly in pigs. The attractiveness of this suggestion lies in the fact that if food intake during health challenges

can be predicted, growth follows on the basis of the principles of mass and energy conservation outlined above.

When predicting the performance of animals under health challenging conditions there are additional problems to resolve. The challenged animal will need to: 1) divert nutrient resources towards the repair of the damaged tissue (e.g., digestive tract for gastrointestinal pathogens and lung for respiratory pathogens, Coop and Kyriazakis (1999)); 2) direct nutrient resources towards the function of immune response, which is the mechanism through which the animal eventually overcomes the pathogen (Kyriazakis and Houdijk, 2007). There is also the need to predict the consequences of the health challenge on the ability of the animal to digest and utilise its food (Escobar *et al.*, 2002). The usual proposed solution to these problems is to assume that resource requirements for (1) and (2) can be represented as increases in maintenance requirements; the remaining resources are then allocated to growth according to the principles detailed above (Kyriazakis and Houdijk, 2007; Sandberg *et al.*, 2006). There are more elaborate mechanisms that have been assumed to apply to the partitioning of nutrient resources in animals subjected to health challenges (Berk *et al.*, 2016; Doeschl-Wilson *et al.*, 2008; Laurenson *et al.*, 2011). Predicting the limitations in the growth of animals with altered health status remains one of the most challenging fields of research in modelling to date.

5. Animal response to increased availability of resources for growth

In the above sections, different types of resource limitation that restrict animal growth have been discussed. A remaining question is: what will happen to the animal if these limitations are removed (i.e., access to resources is returned to a 'normal' level, or, changed to a higher level, see Figure 3B). This is of particular practical relevance as environmental conditions within a production system may vary; for example, animals may be affected by a pathogen, but they may either be treated or overcome its consequences through the development of an immune response. This will impose growth limitations over a long or a short period of time. In theory, the growth of the animal under such conditions may follow one of three patterns, compared to an animal of a similar initial size that has not been exposed to such limitations: 1) the animal will grow at a slower rate; 2) the animal will grow at the same rate; or 3) the animal will grow at a faster rate. There is evidence in the literature that all these outcomes are possible. Pattern 1 was evidenced in the classical experiments of Widdowson and McCance (1963) and Lister and McCance (1967), where pigs with severe limitation in resource provision for a long period of time (up to two years), failed to grow at the same rate as non-constrained counterparts. Moreover, the constrained pigs never reached the mature size of their less constrained siblings or other counterparts. The usual explanation offered for this observation is that the resource limitation imposed on these pigs was so severe that the animals were permanently stunted. Such severe constraint is unlikely to apply in modern pig and broiler production systems and for this reason will not be considered here any further.

On the other hand there is consistent evidence to suggest that short-term limitations and deviations in the growth of animals do not seem to matter in the longer term. The animal is capable of maintaining a growth pattern consistent with Pattern 2, as seen in the experiments of Kyriazakis and Emmans (1990), where the diet composition offered to young pigs changed on a daily basis and their growth was similarly disrupted over the same time scale.

There is considerable evidence to suggest that previously constrained animals are able to show compensation after a limitation in resources is reduced (Pattern 3 described above). The subsequent increase in size can be at a higher rate than that of a similar sized animal that has continuously exhibited growth without the severe constraint in question. This kind of behaviour has been observed in a wide variety of animal species (Kyriazakis and Emmans, 1992c; Metcalfe and Monaghan, 2001). A clear example of this kind of phenomenon can be seen in Figure 2, where the growth of an animal is faster after a restriction in access to feed has been removed, compared to the animal which has not been exposed to such a restriction (Stamataris *et al.*, 1991). This additional growth and recovery in size upon unrestricted access to food, is made possible through a voluntary feed intake that is temporarily increased in relation to the voluntary feed intake of an animal of the same size or age that has always had unrestricted access to food. As a result of this higher growth rate, there are several possibilities regarding the size the recovering animal can reach compared to an animal that has grown under more favourable conditions. It is possible that the recovering animal would eventually reach the same size as animals that have not been exposed to these constraints; while we expect they would not grow bigger than that size, there is no fundamental impediment that they would. It should be noted that the rate of this compensatory growth itself can be limited by many factors, including the availability and composition of feed, and the animal's maximum capacity to ingest food. However, in general the phenomenon of compensatory growth demonstrates that the growth of an animal is flexible, and that there is no single, specific 'maximum' or 'optimum' growth rate even under favourable growth conditions. Instead, as a result of environmental disturbances, the growth of each phenotype can be adjusted either up or down compared to the 'normal' smooth growth pattern described earlier in this chapter.

In livestock production, the existence of compensatory growth has raised some questions. As for many animal production systems, fast growth is one of the main targets of farmers, and therefore they might ask why such a 'higher than normal' growth rate cannot be achieved in standard growing conditions even if the growth conditions are aimed to favour fast growth. In the following, some potential biological explanations for this phenomenon are discussed.

The evolutionary drivers behind compensatory growth have been discussed in detail by Metcalfe and Monaghan (2001). They state that in a variety of animal species, the selection pressure is likely to favour 'increased size-at-age'. As a result, it would be beneficial for an individual that has, for various potential reasons, grown slowly at an early age, to put extra effort into increased feed intake that would allow it to catch up with the growth that would normally have occurred under more favourable conditions. However, this extra effort may be costly for the animal. The authors show a list of different types of costs related to this compensatory growth, including predation risk, disturbed maintenance, increased risk of disease, and reduced lifespan. So the conclusion here might be; as an evolutionary outcome, fast growth is not beneficial for an animal, but not at any cost. Only under exceptional conditions when previous growth has been impaired, can it be useful to utilize the growth at its highest rate.

This brings in the question of how the phenomenon of compensatory growth that has some evolutionary benefits under natural conditions will apply in controlled livestock production and under artificial selection, where the phenomenon has also been observed, but where the benefits and costs might be very different compared to animals in the wild. The ability for compensatory growth certainly has benefits in commercial livestock production, as it would be useful for the

farmers to have the animals grow towards similar size, regardless of whether or not they have had a 'bad start' in their growth cycle (Douglas *et al.*, 2013). In addition, many of the costs of compensatory growth occurring in natural conditions are not relevant in commercial farming, such as predatory risk and reduced life span. Therefore, it can be speculated that the potential for compensatory growth can have even stronger weight in artificial than in natural selection, and can be seen as part of the trait of 'resilience' which is nowadays an important target of breeding programmes. In any case, as mentioned above, the occurrence and magnitude of this growth pattern is highly variable and depends strongly on the timing and severity of the disturbance that limits growth, as well as on the type and developmental stage of the animal itself. Therefore, developing generally applicable predictive models for compensatory growth can be seen as a major challenge for animal science in the future.

From a modelling perspective, a change in growth conditions such those described above poses two challenges. First, as there are distinct periods during which the conditions of growth are approximately constant, a piecewise model is required, as discussed in section 3.2 (Figure 3B). This model elaboration is not difficult to implement provided that growth can be described by the same basic conceptual model in each period (i.e. a sigmoidal growth function). The difficulty here is likely to be in estimating a larger number of parameters, characterising the multiple growth functions and associated time periods, from an amount of data often comparable to that when conditions do not change. This multi-module approach, however, relies on the assumption that the animal responds rapidly to a change, or at least that growth is described by a similar growth model before and after the change. The second challenge, therefore, is in describing the animal's response to the change when there is a transient pattern in the response that has taken long enough not to be negligible, prior to the settling of growth into a sigmoidal pattern. Addressing this problem may or may not require an understanding of the mechanisms driving the animal's response to the change, depending on whether a prediction of growth under extrapolated conditions is required.

6. Concluding remarks

In presenting a set of principles for a quantitative description of animal growth, we have addressed growth as a three-faceted problem. We adopted a theoretical framework where these situations are regarded as parts of a whole, encompassing the growth conditions across modern livestock production systems. Sigmoidal growth arises within most situations and time periods where growth conditions are kept approximately constant; the quantitative models of growth in their basic form apply within such periods.

The usefulness of the existing theories and mathematical models depends on the availability of empirical data for testing the hypotheses and parameterising the models over a range of conditions. The research challenge ahead, therefore, is in further testing and consolidating modelling prediction of growth under specified diet, environmental, and health conditions, or as animals respond to changes in limiting conditions. These steps require an increased availability of experimental data collected under a wide range of *in vivo* conditions, and the generation of such data will benefit from the use of novel monitoring technologies with reduced invasiveness. Such technologies are currently being developed within the context of precision livestock farming.

Chapter 13 In: Paul J. Moughan and Wouter H. Hendriks, ed. Feed Evaluation Science. Wageningen: Wageningen Academic Publishers, 2018

The heterogeneity in performance among animals within breeds and herds poses two practical problems; 1) how to manage groups of animals to optimise resource use and performance and reduce waste, and 2) how to characterise traits of animals within a breed to artificially select among phenotypical variation and, in particular, to ensure a tangible level of improvement across farm conditions. Here, it would be particularly relevant to improve the means of identifying and predicting the performance of resilient phenotypes, which could, for example, further increase the use of compensatory growth in commercial farming. We discussed and proposed early steps towards the solution of these problems that involve phenotypical characterisation of populations. Further progress will require a much greater availability of rich individual data, cross-sectioning herds and breeds, which should materialise further in this age of an increasing trend towards precision farming.

Acknowledgements

This work was funded in part by the European Commission (Grant agreement no: 633531) under the EU Framework Programme for Research and Innovation Horizon 2020. The Commission accepts no responsibility or liability whatsoever with regard to the material in this paper. We are grateful to our colleagues Panagiotis Sakkas and Egbert Knol for providing us access to unpublished data.

References

Armsby, H.P. and Moulton, C.R., 1925. The animal as a converter of matter and energy; a study of the role of live stock in food production. Book Department, The Chemical catalog Company, Inc., New York.

Aviagen, 2011. Ross 308 Parent Stock: Performance Objectives.

Aviagen, 2014a. Ross 308 Broiler: Nutrition Specifications.

Aviagen, 2014b. Ross 308 Broiler: Performance Objectives.

Aviagen, 2016. Ross 308 Parent Stock: Nutrition Specifications.

Beaumont, M.A., 2010. Approximate Bayesian Computation in Evolution and Ecology. In: D.J. Futuyma, H.B. Shafer and D. Simberloff (eds.), Annual Review of Ecology, Evolution, and Systematics, Vol 41. Annual Review of Ecology Evolution and Systematics. Annual Reviews, Palo Alto, pp. 379-406.

Berk, Z., Bishop, S.C., Forbes, A.B. and Kyriazakis, I., 2016. A simulation model to investigate interactions between first season grazing calves and Ostertagia ostertagi. Veterinary Parasitology 226: 198-209.

Berman, A. and Snapir, N., 1965. The relation of fasting and resting metabolic rates to heat tolerance in the domestic fowl. British Poultry Science 6: 207-216.

Black, J.L., Giles, L.R., Wynn, P.C., Knowles, A.G., Kerr, C.A., Jones, M.R., Strom, A.D., Gallagher, N.L. and Emmens, G.J., 2001. A review - Factors limiting the performance of growing pigs in commercial environments. In: P.D. Cranwell (ed.), Manipulating pig production Viii, Proceedings. Australasian Pig Science Association (Apsa) - Conference Proceedings. Australasian Pig Science Assoc, Werribee, pp. 9-36.

Brown, D. and Mount, L.E., 1982. The metabolic body size of the growing-pig. Livestock Production Science 9: 389-398.

Burdge, G.C., Hanson, M.A., Slater-Jefferies, J.L. and Lillycrop, K.A., 2007. Epigenetic regulation of transcription: a mechanism for inducing variations in phenotype (fetal programming) by differences in nutrition during early life? British Journal of Nutrition 97: 1036-1046.

Coop, R.L. and Kyriazakis, I., 1999. Nutrition-parasite interaction. Veterinary Parasitology 84: 187-204.

de Lange, C.F.M., Morel, P.C.H. and Birkett, S.H., 2003. Modeling chemical and physical body composition of the growing pig. Journal of Animal Science 81: E159-E165.

Doeschl-Wilson, A.B., Vagenas, D., Kyriazakis, I. and Bishop, S.C., 2008. Exploring the assumptions underlying genetic variation in host nematode resistance (Open Access Publication). Genetics Selection Evolution 40: 241-264.

Douglas, S.L., Edwards, S.A., Sutcliffe, E., Knap, P.W. and Kyriazakis, I., 2013. Identification of risk factors associated with poor lifetime growth performance in pigs. Journal of Animal Science 91: 4123-4132.

Emmans, G. and Kyriazakis, I., 2001. Consequences of genetic change in farm animals on food intake and feeding behaviour. Proceedings of the Nutrition Society 60: 115-125.

Emmans, G.C., 1984. An additive and linear energy scale. Animal Production 38: 538-538.

Emmans, G.C., 1994. Effective energy - a concept of energy-utilization applied across species. British Journal of Nutrition 71: 801-821.

Emmans, G.C., 1997. A method to predict the food intake of domestic animals from birth to maturity as a function of time. Journal of Theoretical Biology 186: 189-199.

Emmans, G.C. and Fisher, C., 1986. Problems in nutritional theory. In: C. Fisher and K.N. Boorman (eds.), Nutrient Requirements of Poultry and Nutritional Research. Butterworths, London, pp. 9 – 39.

Emmans, G.C. and Kyriazakis, I., 1995. A general-method for predicting the weight of water in the empty bodies of pigs. Animal Science 61: 103-108.

Emmans, G.C. and Kyriazakis, I., 1997. Models of pig growth: problems and proposed solutions. Livestock Production Science 51: 119-129.

Emmans, G.C. and Oldham, J.D., 1988. Modelling of growth and nutrition in different species. In: S. Korver, J.A.M. van Arendonk (ed.), Modelling of livestock production systems. Kluwer Academic Publishers, Amsterdam, pp. 13-21.

Escobar, J., Van Alstine, W.G., Baker, D.H. and Johnson, R.W., 2002. Growth performance and whole-body composition of pigs experimentally infected with Mycoplasma hyopneumoniae. Journal of Animal Science 80: 384-391.

Ferguson, N.S., Gous, R.M. and Emmans, G.C., 1994. Preferred components for the construction of a new simulation-model of growth, feed-intake and nutrient-requirements of growing pigs. South African Journal of Animal Science-Suid-Afrikaanse Tydskrif Vir Veekunde 24: 10-17.

Ferguson, N.S., Gous, R.M. and Emmans, G.C., 1997. Predicting the effects of animal variation on growth and food intake in growing pigs using simulation modelling. Animal Science 64: 513-522.

Ferguson, N.S. and Kyriazis, S.T., 2003. Evaluation of the growth parameters of six commercial crossbred pig genotypes - 1. Under commercial housing conditions in individual pens. South African Journal of Animal Science 33: 11-20.

Gelman, A., Carlin, J.B. and Stern, H.S., 2013. Bayesian data analysis. Chapman & Hall/CRC Press, Boca Raton, Fla.; London; New York, N.Y.

Huxley, J., 1932. Problems of relative growth. Lincoln MacVeagh, The Dial Press, New York.

Knap, P.W., 2000a. Stochastic simulation of growth in pigs: relations between body composition and maintenance requirements as mediated through protein turn-over and thermoregulation. Animal Science 71: 11-30.

Knap, P.W., 2000b. Time trends of Gompertz growth parameters in 'meat-type' pigs. Animal Science 70: 39-49.

Knap, P.W., Roehe, R., Kolstad, K., Pomar, C. and Luiting, P., 2003. Characterization of pig genotypes for growth modeling. Journal of Animal Science 81: E187-E195.

Kyriazakis, I., 1989. Growth, feed intake and diet selection in pigs: theory and experiments. PhD Thesis, University of Edinburgh, Edinburgh.

Kyriazakis, I., 2014. Pathogen-induced anorexia: a herbivore strategy or an unavoidable consequence of infection? Animal Production Science 54: 1190-1197.

Kyriazakis, I., Dotas, D. and Emmans, G.C., 1994. The effect of breed on the relationship between feed composition and the efficiency of protein-utilization in pigs. British Journal of Nutrition 71: 849-859.

Kyriazakis, I. and Emmans, G.C., 1990. The immediate effects of abrupt diet composition changes in young-pigs. British Journal of Nutrition 64: 619-623.

Kyriazakis, I. and Emmans, G.C., 1992a. The effects of varying protein and energy intakes on the growth and body-composition of pigs .1. the effects of energy-intake at constant, high protein-intake. British Journal of Nutrition 68: 603-613.

Kyriazakis, I. and Emmans, G.C., 1992b. The effects of varying protein and energy intakes on the growth and body-composition of pigs. 2. the effects of varying both energy and protein-intake. British Journal of Nutrition 68: 615-625.

Kyriazakis, I. and Emmans, G.C., 1992c. The growth of mammals following a period of nutritional limitation. Journal of Theoretical Biology 156: 485-498.

Kyriazakis, I. and Houdijk, J.G.M., 2007. Food intake and performance of pigs during health, disease and recovery. In: J. Wiseman, M.A. Varley, S. McOrist and B. Kemp (eds.), Paradigms in pig science. Nottingham University Press, Nottingham, pp. 493-513.

Kyriazakis, I. and Whittemore, C.T., 2005. Whittemore's science and practice of pig production|Science and practice of pig production. Blackwell Science, Oxford.

Laurenson, Y., Bishop, S.C. and Kyriazakis, I., 2011. In silico exploration of the mechanisms that underlie parasite-induced anorexia in sheep. British Journal of Nutrition 106: 1023-1039.

Letourneau-Montminy, M.P., Narcy, A., Dourmad, J.Y., Crenshaw, T.D. and Pomar, C., 2015. Modeling the metabolic fate of dietary phosphorus and calcium and the dynamics of body ash content in growing pigs. Journal of Animal Science 93: 1200-1217.

Lister, D. and McCance, R.A., 1967. Severe undernutrition in growing and adult animals. 17. The ultimate results of rehabilitation: pigs. The British Journal of Nutrition 21: 787-799.

Metcalfe, N.B. and Monaghan, P., 2001. Compensation for a bad start: grow now, pay later? Trends in Ecology & Evolution 16: 254-260.

Montes, L., de Margerie, E., Castanet, J., de Ricqles, A. and Cubo, J., 2005. Relationship between bone growth rate and the thickness of calcified cartilage in the long bones of the Galloanserae (Aves). Journal of Anatomy 206: 445-452.

Moughan, P.J., Smith, W.C. and Stevens, E.V.J., 1990. Allometric growth of chemical body components and several organs in the pig (20-90 kg liveweight). New Zealand Journal of Agricultural Research 33: 77-84.

Noblet, J., Karege, C., Dubois, S. and van Milgen, J., 1999. Metabolic utilization of energy and maintenance requirements in growing pigs: Effects of sex and genotype. Journal of Animal Science 77: 1208-1216.

Pomar, C., Kyriazakis, I., Emmans, G.C. and Knap, P.W., 2003. Modeling stochasticity: Dealing with populations rather than individual pigs. Journal of Animal Science 81: E178-E186.

Reed, K.F., Arhonditsis, G.B., France, J. and Kebreab, E., 2016. Technical note: Bayesian calibration of dynamic ruminant nutrition models. Journal of Dairy Science 99: 6362-6370.

Richards, F.J., 1959. A flexible growth function for empirical use. Journal of Experimental Botany 10: 290-300.

Robertson, T.B., 1908. On the normal rate of growth of an individual, and its biochemical significance. Archiv fuer Entwicklungsmechanik Leipzig 25: 581-614.

Sandberg, F.B., Emmans, G.C. and Kyriazakis, I., 2006. A model for predicting feed intake of growing animals during exposure to pathogens. Journal of Animal Science 84: 1552-1566.

Sandilands, V., Tolkamp, B.J., Savory, C.J. and Kyriazakis, I., 2006. Behaviour and welfare of broiler breeders fed qualitatively restricted diets during rearing: Are there viable alternatives to quantitative restriction? Applied Animal Behaviour Science 96: 53-67.

Schmidt-Nielsen, K., 1984. Scaling, why is animal size so important? Cambridge University Press, Cambridge; New York.

Sivia, D.S. and Skilling, J., 2006. Data analysis : a Bayesian tutorial. Oxford University Press, Oxford; New York.

Stamataris, C., Kyriazakis, I. and Emmans, G.C., 1991. The performance and body-composition of young-pigs following a period of growth-retardation by food restriction. Animal Production 53: 373-381.

Strathe, A.B., Danfaer, A., Sorensen, H. and Kebreab, E., 2010. A multilevel nonlinear mixed-effects approach to model growth in pigs. Journal of Animal Science 88: 638-649.

Strathe, A.B., Jorgensen, H., Kebreab, E. and Danfaer, A., 2012. Bayesian simultaneous equation models for the analysis of energy intake and partitioning in growing pigs. Journal of Agricultural Science 150: 764-774.

Symeou, V., Leinonen, I. and Kyriazakis, I., 2014a. Modelling phosphorus intake, digestion, retention and excretion in growing and finishing pig: model evaluation. Animal 8: 1622-1631.

Symeou, V., Leinonen, I. and Kyriazakis, I., 2014b. Modelling phosphorus intake, digestion, retention and excretion in growing and finishing pigs: model description. Animal 8: 1612-1621.

Symeou, V., Leinonen, I. and Kyriazakis, I., 2016. The consequences of introducing stochasticity in nutrient utilisation models: the case of phosphorus utilisation by pigs. British Journal of Nutrition 115: 389-398.

van Milgen, J., Valancogne, A., Dubois, S., Dourmad, J.Y., Seve, B. and Noblet, J., 2008. InraPorc: A model and decision support tool for the nutrition of growing pigs. Animal Feed Science and Technology 143: 387-405.

Vautier, B., Quiniou, N., van Milgen, J. and Brossard, L., 2013. Accounting for variability among individual pigs in deterministic growth models. Animal 7: 1265-1273.

Wellock, I.J., Emmans, G.C. and Kyriazakis, I., 2003a. Modelling the effects of thermal environment and dietary composition on pig performance: model logic and concepts. Animal Science 77: 255-266.

Wellock, I.J., Emmans, G.C. and Kyriazakis, I., 2003b. Predicting the consequences of social stressors on pig food intake and performance. Journal of Animal Science 81: 2995-3007.

Wellock, I.J., Emmans, G.C. and Kyriazakis, I., 2004. Describing and predicting potential growth in the pig. Animal Science 78: 379-388.

Whittemore, C.T., Tullis, J.B. and Emmans, G.C., 1988. Protein-growth in pigs. Animal Production 46: 437-445.

Whittemore, E.C., Emmans, G.C. and Kyriazakis, I., 2003a. The problem of predicting food intake during the period of adaptation to a new food: a model. British Journal of Nutrition 89: 383-398.

Whittemore, E.C., Emmans, G.C. and Kyriazakis, I., 2003b. The relationship between live weight and the intake of bulky foods in pigs. Animal Science 76: 89-100.

Widdowson, E.M. and McCance, R.A., 1963. The effect of finite periods of undernutrition at different ages on the composition and subsequent development of the rat. Proceedings of the Royal Society of London. Series B, Biological Sciences 158: 329-342.

Winsor, C.P., 1932. The Gompertz curve as a growth curve. Proceedings of the National Academy of Sciences of the United States of America 18: 1-8.

Zhai, H. and Adeola, O., 2013a. True digestible phosphorus requirement for twenty- to forty-kilogram pigs. Journal of Animal Science 91: 5307-5313.

Zhai, H. and Adeola, O., 2013b. True digestible phosphorus requirement of 10- to 20-kg pigs. Journal of Animal Science 91: 3716-3723.

Zhai, H. and Adeola, O., 2015. True digestible phosphorus requirement for forty- to eighty-kilogram pigs. Journal of Animal Science 93: 5711-5717.

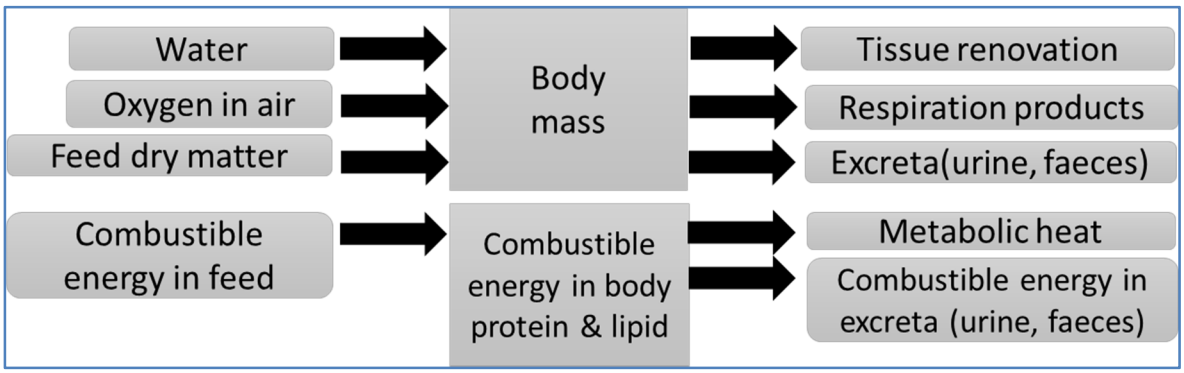

Figure 1. Principal mass and energy inputs and outputs during animal growth.

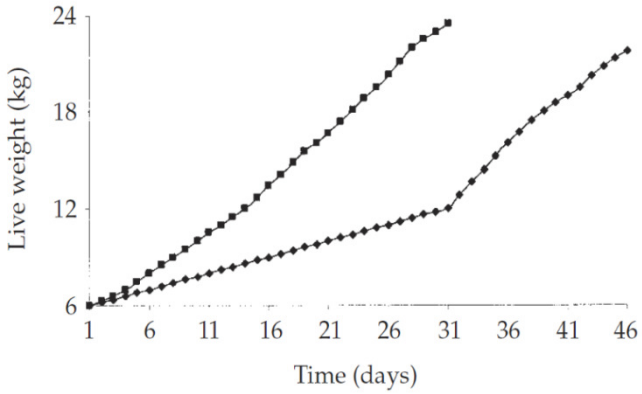

Figure 2. Typical live weight against time (since start of experiment) for growing pigs. The pigs were given *ad libitum* access to a high quality feed (■) or restricted access to the same feed up to 12 kg live weight and *ad libitum* access thereafter (♦). Reproduced with permission from Stamataris *et al.* (1991).

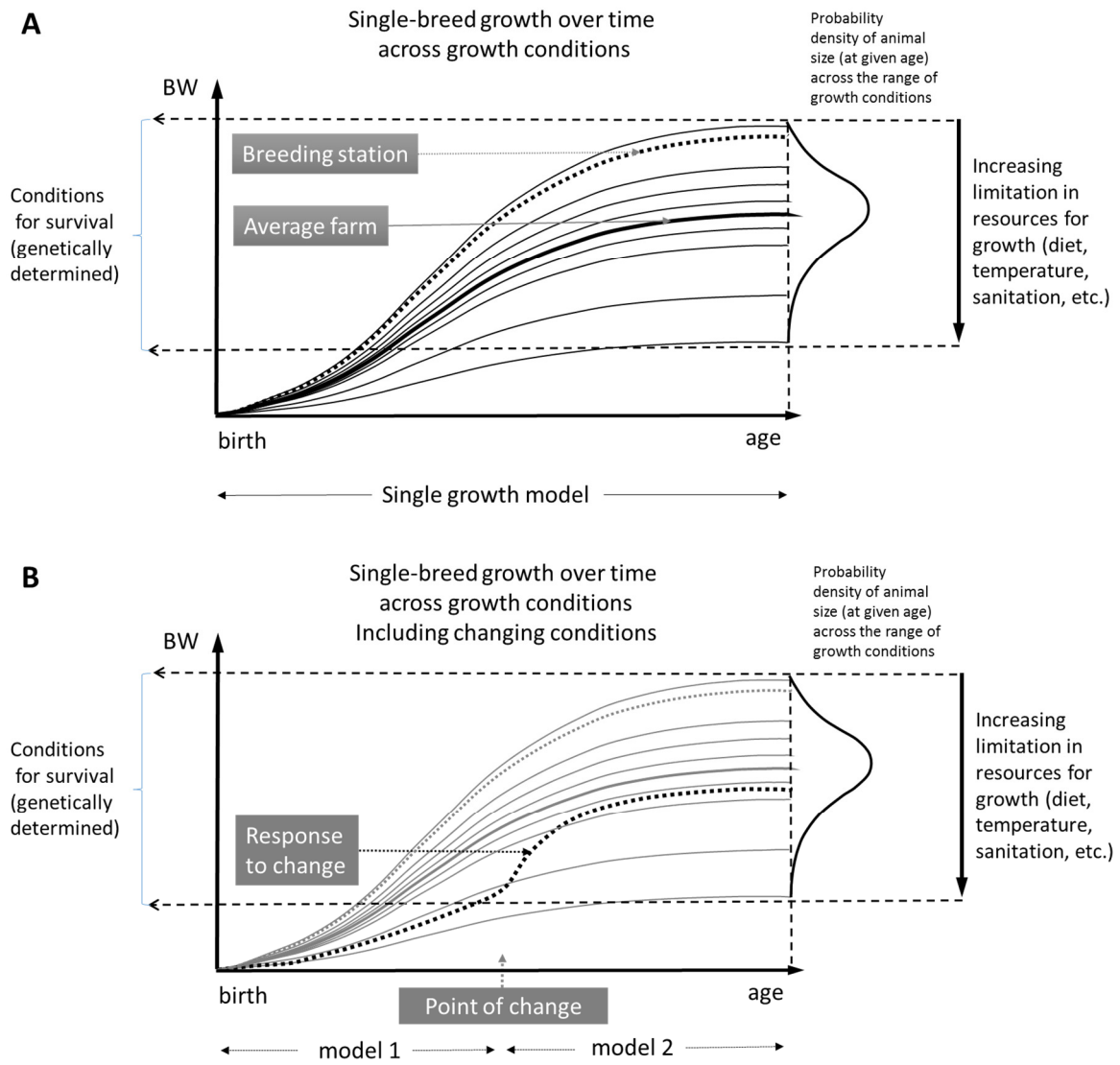

Figure 3. Theoretical framework for describing growth conditions across livestock systems and resulting growth patterns for a given breed of animal. A) Stable (or approximately stable) growth conditions (see text). B) Animal response to a strong change in growth conditions is to switch to a different regimen of sigmoidal growth. Each sigmoidal curve represents animal size (body weight, BW); the different curves represent growth across conditions with increasing limitation in resources for growth; the spectrum of conditions has an associated probability density between two genetically-determined bounds. Conditions in a breeding station approach (but do not reach) those of maximum performance. Average farm performance is in the region of average conditions.

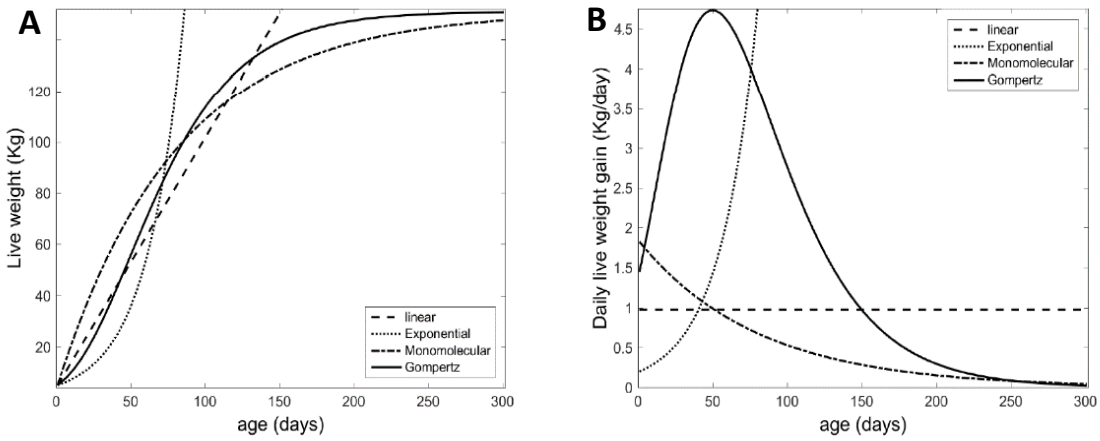

Figure 4. **Illustration of hypothetical models of growth of live weight**. A) Unbounded growth where live weight is ever increasing with age (linear and exponential, Equations (6) and (8)) and limited growth where the animal reaches a limit size at maturity (monomolecular and Gompertz, Equations (10) and (12)). B) Growth rate (daily increase in live weight, defined in Equations (5), (7), (9), (11)) corresponding to the same models and same parameter values (defined in Equations (6), (8), (10), (12)) as in A. A point of maximum growth after birth (inflection point) only exists in the Gompertz model and occurs at ~1/3 of maturity.

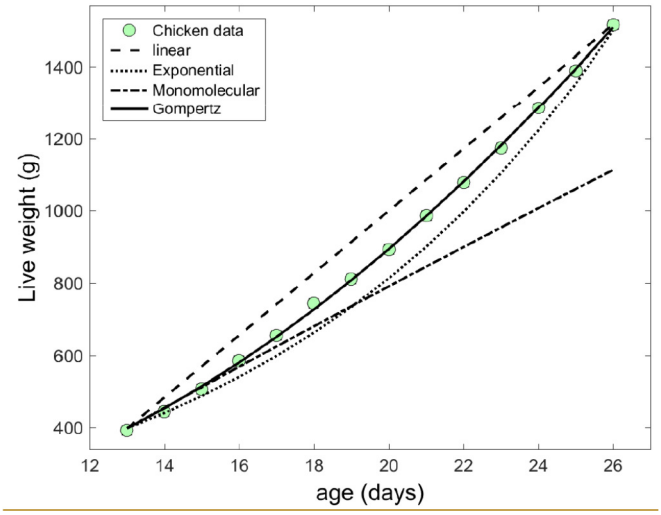

Figure 5. **Four growth models fitted to live weight data**.) Live weight of growing broilers between 13 and 26 days of age. The growth models are the same as in Figure 4 but with fitted parameter values. Only the Gompertz model has sigmoidal shape and fits the data well. Data courtesy of Panagiotis Sakkas.

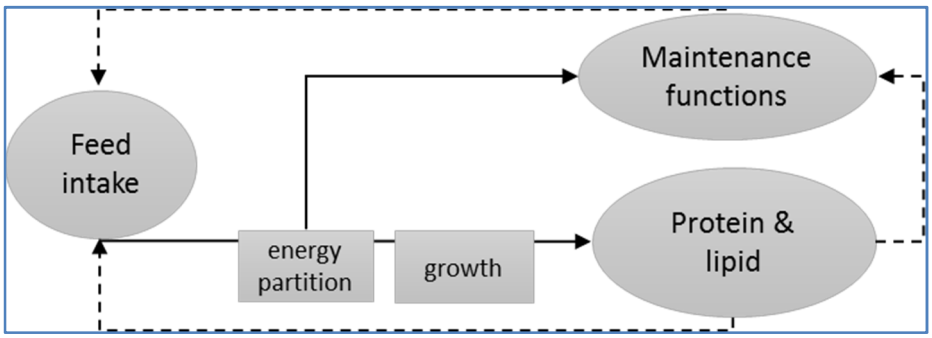

Figure 6. **Principal energy flows associated with the growth of the body mass components of an animal**. The energy flow involved in the maintenance functions is lost heat. Broken lines represent feedback and regulatory processes not explicit in basic models of growth.

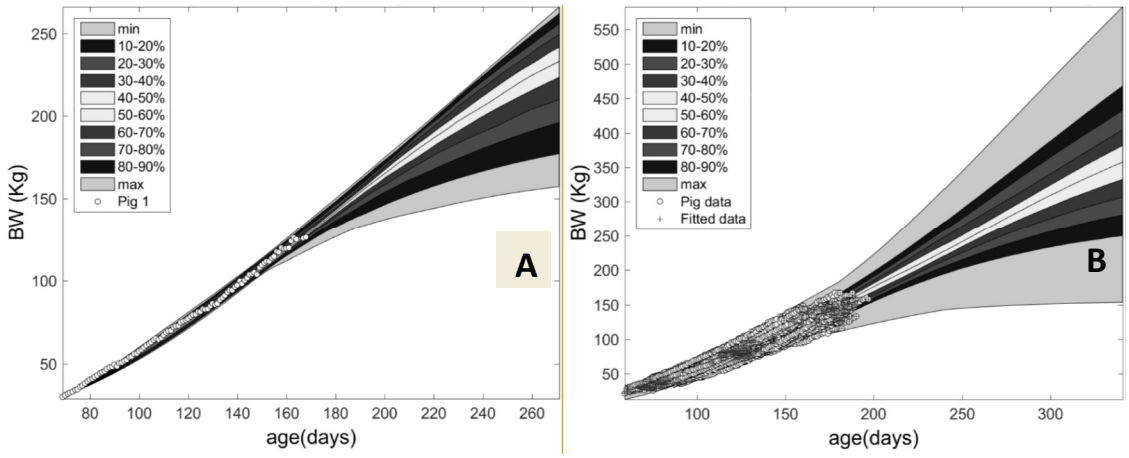

Figure 7. **Predicted distributions of live weight for growing pigs from a single breed**. A) An individual pig. B) Population of pigs. The Gompertz growth model (12) was fitted from the age of first observation through the mid and last data points for each animal and a posterior distribution of Gompertz parameters was generated for: A) an individual pig, B) a population of pigs (not shown). By sampling parameters from the latter and simulating the model for each sample, a predicted posterior distribution of body weight was generated from 30 days, through 180 days (maximum age observed) up to 360 days. The distribution for 180-360 days is predicted without supporting data (extrapolated) in that age range, which is reflected in the increased spread (uncertainty) in the predicted distribution. Empirical data provided by Topigs Norsvin.

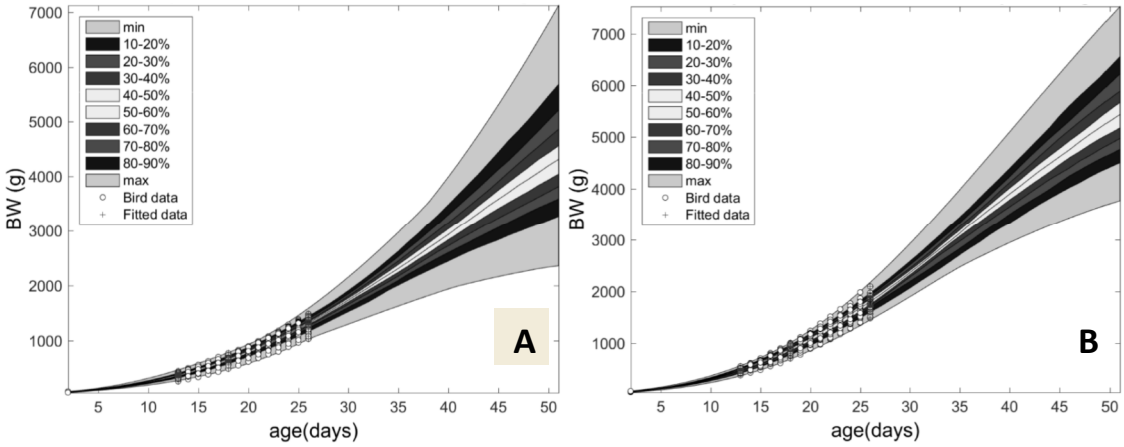

Figure 8. **Predicted distributions of live weight of growing chickens (broilers) for two breeds**. A) slower-growing breed. B) faster-growing breed. The distribution was generated as in Figure 7, but here the data ranged from 13 to 26 days, and the model was simulated from day 2 (for which the live weight of each animal was observed), through day 26, up to day 52. The distribution for 26-52 days is predicted without supporting data (extrapolated) in that age range, which is reflected in the increased spread (uncertainty) in the predicted distribution. Experimental data provided by Panagiotis Sakkas.

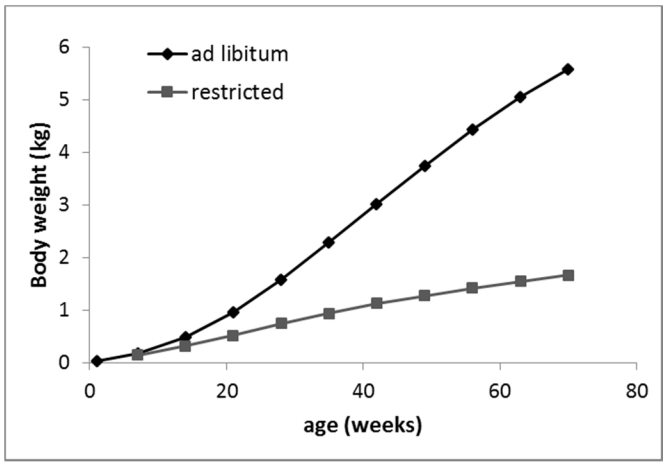

Figure 9. Growth of birds with different levels of access to food. The expected growth of a male broiler bird (*ad libitum* feeding) and a male parent bird (restricted feeding) of the same breed (Ross 308) according to the performance objectives provided by the breeding company (Aviagen 2011, 2014a).

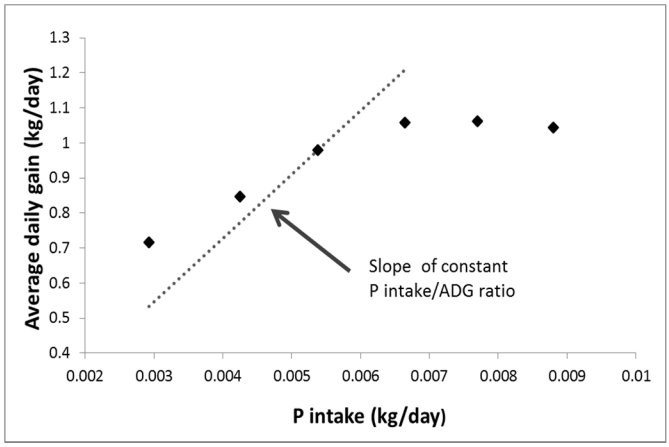

Figure 10. Relationship between daily gain and digestible phosphorus intake in pigs. The broken line indicates the hypothetical gain under conditions where the daily gain:phosphorus retention ratio would remain constant. Data from Zhai and Adeola (2015).